Reference: *Biol. Bull.* **165**: 305–320. (August, 1983)

ON THE EVOLUTIONARY CONSTRAINT SURFACE OF HYDRA

L. B. SLOBODKIN AND KENNETH DUNN

Department of Ecology and Evolution, State University of New York, Stony Brook, L.I., NY 11794

Abstract

Food consumption, body size, and budding rate were measured simultaneously in isolated individual hydra of six strains. For each individual hydra the three measurements define a point in the three dimensional space with axes: food consumption, budding rate, and body size. These points lie on a single surface, regardless of species. Floating rate and incidence of sexuality map onto this surface. We suggest that this surface is an example of a general class of evolutionary constraint surfaces derived from the conjunction of evolutionary theory and the theory of ecological resource budgets. These constraint surfaces correspond to microevolutionary domains.

Introduction

While there may be many conceivable solutions to the ecological and evolutionary problems faced by organisms, not all of these solutions are equally practicable from the standpoint of the organisms themselves (Wright, 1932). An ideally designed organism, able to meet all contingencies, need neither evolve nor reproduce. However, organisms are constrained in their structure and capacities as if, as noted by Bateson (1963), there were an "economics" of somatic response and evolution. As a rule, while the existence of these constraints is accepted, they cannot be explicitly and completely described for any group of organisms, due primarily to gaps in our knowledge of natural history and development. As a rule, properties to be studied are selected for either interest or convenience and there is no attempt at explicitly describing any organism's complete evolutionary strategy (in the sense of Slobodkin and Rapoport, 1974, and Plotkin and Odling-Smee, 1981). This is due, in part, to the inherent complexity of most organisms.

Hydra seemed simple enough in anatomy and sufficiently restricted in their behavior to facilitate an attempt at a reasonably complete explicit description and quantitative analysis of evolutionary restrictions. We present part of this description here. Further descriptive experiments are underway and a mathematical analysis, suggested by the descriptive work to date, is being developed by Gatto, Matessi, and Slobodkin (in prep.).

Hydra are generally similar in shape. Species differ in body size, budding rate, and the presence or absence of symbiotic algae. The spectrum of physiological and behavioral responses does not differ markedly among hydra species, but they do differ in the circumstances which elicit these responses. It was hypothesized by Slobodkin (1979) that perhaps all individual hydra, regardless of species, could be considered to show the same basic patterns of growth and development, differing only in the way that a given amount of food energy is partitioned between the maintenance of the adult's body and reproduction.

This hypothesis was presented in geometric form as a curved surface in a three

Received 14 February 1983; accepted 25 May 1983.

dimensional space, with the axes steady-state body size, steady-state budding rate, and food consumption. In Slobodkin (1979) this was referred to as an "Adaptive Response Surface." Since then the word "Adapted", and its etymological relatives, have become embroiled in almost polemical discussions. We would therefore prefer to use the term "Constraint" Surface. The term "steady-state" restricts predictions to hydra individuals that have had a relatively constant food supply for long enough that neither body size nor budding rate are changing. It is implicitly assumed that senescence does not occur in hydra. That is, any hydra, regardless of species was assumed to lie on a two-dimensional surface in the space defined by the three dimensions body size, food income, and budding rate. This hypothetical surface is shown in Figure 1.

The hypothesis also asserts that either a clone of hydra in which a series of individuals are each equilibrated to a different food level or a single individual with a very slowly changing food supply, will trace a line on the surface. The animals are assumed to have already completed their transition from bud to potentially reproductive adult.

The shape of the surface takes account of the well known fact that budding rate increases with food consumption of individual hydra, that larger hydra species reproduce more slowly than smaller ones at any given food supply, and that hydra stop budding and become smaller when starved (Slobodkin, 1964; Stiven, 1965; Hecker and Slobodkin, 1976; Gurkewitz *et al.*, 1980; i.a.).

It is not tautological that a single surface should account for the variation between hydra species. It is possible to imagine, for example, that all hydra partition energy

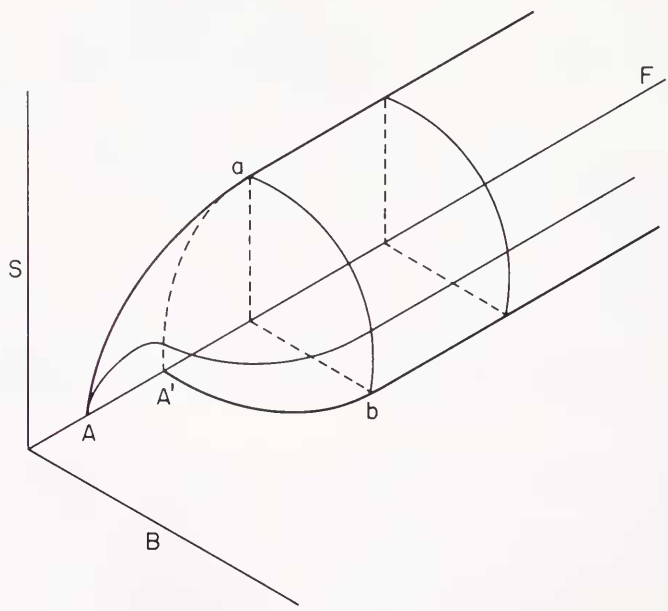

FIGURE 1. A surface relating body size, budding rate, and food supply for all species of hydra, hypothesized by Slobodkin (1979). Each meridional line represents the locus of a particular genotype in the size, budding rate, and food space. The possible states of individuals of a particular species would be represented by a stripe on this surface, covering several such lines. It is assumed that below some food level, A, all hydra will die of starvation. It is further assumed that there exists a food level A′, such that at food levels between A and A′, even the smallest species are considered unable to reproduce.

between growth and reproduction but that the efficiency of the growth and reproductive processes themselves differ between species or with age. If this were so we would expect a cloud of points in three dimensional space, whose upper bound might be similar to Figure 1. To be on a single surface requires that the organisms be relatively constant in efficiency and that a sufficient number of dimensions has been considered.

Several questions are immediately apparent:

1. Is there in fact such a surface?
2. If the surface does exist, can we map significant physiological or ecological properties on it?
3. What are the theoretical implications of positive answers to 1 and 2 with reference to hydra and other organisms?

These questions will be considered in turn, after consideration of our methods.

Materials and Methods

The experimental animals were taken from a variety of strains all of which are being maintained in our laboratory. All of the strains had been in the laboratory for at least a year prior to the start of the experiments, some as long as ten years. Green hydra were represented by a small strain collected in the Nissequogue River on Long Island. Studies on other properties of this strain are discussed in Bossert and Slobodkin (1983). *Hydra americana* were from the laboratory of Richard D. Campbell, as were *Hydra cauliculata*. *Hydra fusca* were from Lago Maggiore, Italy. There was also a very large strain ("Connetquot") from the Connetquot River, Long Island and a slightly smaller brown hydra ("5-tentacle") from the Carmans River, Long Island. These animals are available to investigators on request. We have not attempted rigorous identification of the wild caught strains, since our experiments refer to the genus *Hydra* in its entirety. These strains have persisted in having different sizes and slightly different coloration over many months of culture under closely similar conditions.

M solution was used for all stocks and experimental animals (Lenhoff and Brown, 1970). The animals were maintained in controlled temperature chambers under constant overhead illumination at seventeen degrees centigrade. The experimental animals were fed *ad lib* with *Artemia* nauplii. The *Artemia* nauplii had been hatched within twenty-four hours and washed briefly in distilled water, before being suspended in M solution and offered to the hydra.

Experimental hydra were maintained as isolated individuals in the laboratory for periods of from three weeks to two months. They were offered large numbers of *Artemia* nauplii as food and after each feeding the number of nauplii actually ingested was determined by shining light through the gastric region and counting them in the gastric cavity. The feeding counts were made after the animals had stopped "swallowing" but before digestion made counting too difficult.

To estimate size of the hydra, the animals were photographed. All photographs were taken prior to feeding. The photographic procedure was constant and standard throughout. The single lens reflex camera was on a permanent frame used for this purpose only. Focus and enlargement were not changed. Standards were photographed at each photography session to check on the possibility of inadvertant rearrangements of the apparatus. The length and area were measured using a brightness thresholding algorithm on computer digitized video images of photographic

negatives, which is part of an optical measurement computing program, SPOT, under development by Rohlf and Ferson, at Stony Brook.

One source of error in this procedure is that moribund tissue at the pedal end of a hydra need not be sloughed off immediately. A sausage-like post-peduncle may persist for a while and then drop off quite suddenly. This occurs most often in the larger species.

While every effort was made to standardize the state of contraction of the hydra during the photography, there was the possibility of a major source of error being introduced by differences in contractile state. We assumed that each hydra was a constant volume cylinder lying on its side so that projected area would be a function of length. The relevant equation is:

$$\ln A = \tfrac{1}{2}(\ln V + \ln 4 - \ln \pi + \ln l)$$

in which l is the observed length, A is projected area, and V is the constant volume.

When a series of photographs of hydra individuals in different contractile states was made it was found that the curves of area against length for individual animals of all species conform to this simple equation. The average of the slopes of the relation between log length and log projected area for eleven animals of three species was .514 with standard deviation ± .0110 with an average coefficient of determination of .95 ± .0122. With the apparent verification of the above model, volume can be computed. This measure of volume, being demonstrably independent of contractile state, was taken as our size estimate. Mass, determined as freeze-dried weight, was found to correlate well with calculated volume (Fig. 2).

Budding rate could be immediately determined, since animals were maintained in isolation. Ambiguity was avoided by counting buds after they have dropped off their mothers and using an average budding rate over the period of observation. Other times of origin of buds, as for example, appearance of first tentacles etc., could have been considered without changing things, since there is effectively no death of buds. Any buds that were on animals at the initiation of the period of experimental

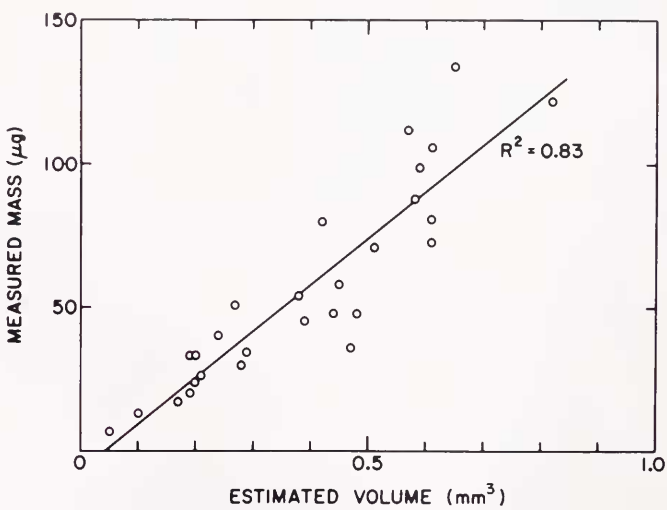

FIGURE 2. The relation between estimated volume, based on a single photograph for each animal, and freeze dried mass of 28 hydra weighed individually on a Cahn Electronic Microbalance.

observation were not included in the bud counts, but buds that were attached at the time of termination of the experiment were included.

Floating and sexuality were noted for one subset of experimental animals.

Notice that the animals had all been taken from stock cultures, so that there was a non-equilibrated transition period during the early portion of their history in isolation. Also we have no guarantee that all animals equilibrated during the observation period. One set of animals was maintained under experimental conditions for ten days and the remainder for twenty-one days prior to the first collecting of data. Rather than arbitrarily omitting data, all of the data were used, and the non-equilibrium may be assumed to have added to our variance.

Results

We now return to the questions listed in the Introduction.

1. Is there in fact a surface of the sort indicated?

The series of measurements for each hydra produced a single point (measured as the triplet; mean body size, mean budding rate, and mean feeding rate). It was found that the green hydra were discordant, having excessively high budding rate and body sizes per unit food consumption, in comparison with the brown species. Since it is known (Muscatine, 1961; Slobodkin, 1964; Stiven, 1965;) that green hydra can receive approximately three times as much energy from their algae as from animal food, the measured food consumption of the green hydra was multiplied by four and the product was used as our estimate of their food consumption. A similar procedure was followed in Slobodkin, (1964). This is obviously a first approximation, and may also have introduced variance. We are now performing experiments designed to estimate the fraction of energy that actually comes from algae under different circumstances. (See also Bossert and Slobodkin, 1983.)

The data for each animal are presented in Table I, and as a three dimensional graph in Figure 3.

The complete set of points using a total of 39 hydra of six strains was tested for fit to a two-dimensional surface embedded in three space.

While the shape of the surface will prove of importance (cf. Gatto, Matessi and Slobodkin, in prep.), our immediate concern is the presence or absence of a surface, rather than its precise shape.

Consider a resource budget consisting of a set of mutually exclusive ways of expending resources, which sum to the total resources income. In our case, bud production and body size maintenance are the result of these expenditures. The resources expended for bud production plus those expended in body maintenance are assumed to equal total resource income. If different strains of hydra apportion resources differently between these expenditures, but the efficiencies are constant between strains (*i.e.,* body size per unit resource expended for body maintenance and buds per unit resource alloted to bud production), then the measurements of individual hydra will generate a monotonic surface in the space whose dimensions consist of an axis for resource income and an axis for each of the modes of expenditure. The term "monotonic surface" requires definition in the present context. The intuitive meaning is of a surface with neither hills nor valleys. In three dimensional space a monotonic surface, in our sense, is one in which the locus of the points of intersection between the surface itself and any flat plane that intersects the axis of resource income will be a monotonic curve passing through the origin.

If the surface in Figure 1 is a monotonic plane folded in three space, rankit

TABLE I

Data for individual hydra

STRAIN	INDI-VIDUAL	# OF DAYS	# OF PHOTOS	MM^3 MEAN SIZE	MEAN FEED	MEAN BUD	OBSERVED DAYS SEXUAL	OBSERVED DAYS FLOATING	NUMBER OBSERVED	FEEDINGS/ WEEK	FOOD/ MEAL
CAULICULATA	1	62	5	.4048	3.613	.2581			25	2.82	8.96
	2	62	7	.4023	4.339	.3065			25	2.82	10.76
	3	62	6	.4341	3.774	.3065			25	2.82	9.36
	4	62	5	.4533	3.726	.2742			25	2.82	9.24
	5	39	6	.3912	6.026	.2632	0	0	12	2.15	19.58
	6	39	6	.2604	3.974	.1842	0	0	12	2.15	12.92
	7	39	6	.3064	4.462	.2368	0	0	12	2.15	14.50
	8	39	6	.3327	6.667	.2105	0	0	12	2.15	21.67
NISSEQUOGUE	1	62	7	.3877	4.452*	.2903			25	2.82	11.04
	2	62	7	.3782	6.065*	.3871			25	2.82	15.04
	3	62	8	.4631	7.419*	.5323			25	2.82	18.40
	4	62	8	.3405	4.258*	.2419			25	2.82	10.56
	5	28	4	.1662	3.286*	.3571	0	0	9	2.25	10.22
	6	14	2	.2438	7.143*	.3571	2	0	5	2.50	9.20
	7	25	4	.1629	4.160*	.1667	0	0	7	1.96	14.86
	8	25	2	.2884	5.120*	.2917	1	0	8	2.24	16.00
AMERICANA	1	62	8	.4115	4.371	.3065			25	2.82	10.84
	2	62	5	.4044	3.935	.2742			25	2.82	9.76
	3	62	8	.3133	3.500	.2742			25	2.82	8.63
	4	62	6	.4085	4.774	.3710			25	2.82	11.84
	5	39	6	.5404	3.692	.2105	7	11	12	2.15	12.00
	6	39	6	.5008	4.410	.1842	11	5	12	2.15	14.33
	7	39	6	.5955	3.256	.2368	9	12	12	2.15	10.58
	8	39	6	.3717	3.231	.1053	11	8	12	2.15	10.50
CONNETQUOT	1	62	8	.7710	3.919	.3065			25	2.82	9.72
	2	62	8	.8864	4.597	.3871			25	2.82	11.40
	3	62	7	.8438	4.629	.3065			25	2.82	11.48
	4	39	6	.6116	4.205	.2105	10	12	12	2.15	13.67
	5	39	6	.6260	3.667	.1579	10	11	12	2.15	11.92
	6	39	6	.5275	3.590	.1579	10	12	12	2.15	11.67
FUSCA	1	62	7	.5524	4.065	.0968			25	2.82	10.08
	2	62	8	.4613	3.258	.1129			25	2.82	8.08
	3	39	6	.5962	3.154	.2105	2	7	12	2.15	10.25
	4	39	6	.7895	2.513	.1579	0	12	12	2.15	8.17
	5	39	6	.4923	3.179	.2105	1	12	12	2.15	10.33
5-TENTACLE	1	39	5	.3584	2.590	.0526	11	11	12	2.15	8.42
	2	39	6	.2620	3.410	.0263	6	5	12	2.15	11.08
	3	39	6	.4680	3.923	.1842	8	7	12	2.15	12.75
	4	39	6	.3515	3.462	.1053	12	2	12	2.15	11.25

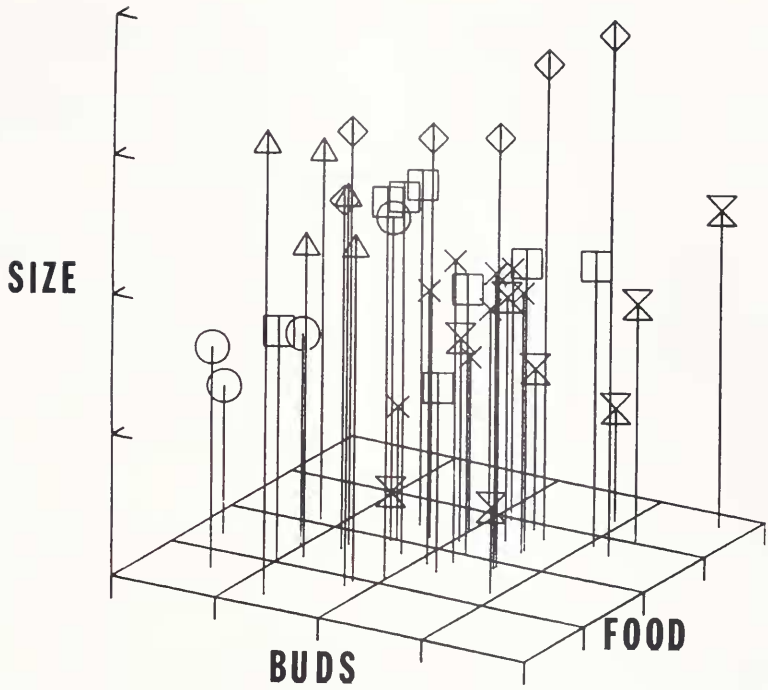

FIGURE 3. Rankit transformed data from Table I, plotted as a three dimensional graph with axes food consumption, body size and budding rate. Both a three dimensional and one dimensional representation of these data can be rejected by Bartlett's test of sphericity at $P > .001$. (Key to symbols—box: *H. americana*, hourglass: Nissequogue strain, triangle: *H. fusca* Italian strain, cross: *H. cauliculata*, diamond: Connetquot strain, circle: 5-tentacle strain).

transformation will project the data onto a flat plane. Principal components analysis and associated tests of significance can then be used to test the fit of the transformed data to a two dimensional surface. The data were therefore converted to rankits (Rohlf and Sokal, 1969). The rankit transformation discards information about the particular shape of the curves relating food, budding rate and size. This transforms any monotonic curve to a plane. The use of rankit transformation in facilitating statistical tests of energy budget data is being addressed, in detail, elsewhere (Wartenburg, Slobodkin and Dunn, in prep.). We assume nothing about the shape of Figure 1 other than its monotonicity.

Principal components for the rankit converted data were calculated using the NTSYS program of Rohlf *et al.* (1982). The first, second, and third eigenvalues and their power to explain variance were 1.627, 1.037, and .3354 with elimination of 54%, 35%, and 11%, respectively, of the data variance.

The rankit data meet the assumptions for Bartlett's Test for Sphericity (Bartlett, 1950; Green and Douglas Carroll, 1978). This test permits assignment of a probability value to the null hypotheses that the data in Figure 3 are adequately represented by a spherical cloud of points (*i.e.*, require three dimensions), or by a cigar shaped cloud varying around a line (*i.e.*, require only one dimension). Both of these hypotheses can be rejected at $P < .001$. That is, we can assert that a three dimensional representation is not necessary, while a one dimensional representation is inadequate, hence we conclude that two dimensions are an appropriate representation.

Departure from three dimensions was checked by Monte Carlo simulation in which the food income, size estimate and budding rate, expressed as rankits, for each hydra were randomized among hydra. The distribution of the resultant triplets was then tested. This was done one hundred times, and the actual, non-randomized data was found to more closely approximate a plane surface than any of these one hundred replicates. We conclude that, in fact, the surface exists.

All of the animals in our experiments were sufficiently well fed to permit budding. We believe that we were in a relatively narrow range of the possible feeding rates. While we intend to study more fully the actual shape of the constraint surface, the region for which we now have data shows a significant correlation between food consumption and budding rate, but not between food consumption and body size. We suggest that hydra more readily adjust their budding rate than their body size to food consumption, once they are sufficiently well fed to bud at all. Otto and Campbell (1977) and Hecker (1978) found that body size does respond to feeding rate at high food levels, and also reported that, at very high food intake rates, hydra may lose the capacity to maintain a steady state in size.

2. Does position on the surface matter to the physiology of the animals?

Slobodkin (1979) suggested that the surface presented in Figure 1 would be divisible into regions, within which hydra would have particular properties. This hypothesis is presented graphically in Figure 4.

At low levels of food intake not only are budding rate and body size reduced but also particular physiological responses are found (Fig. 5).

Large individuals float more readily (see Lomnicki and Slobodkin, 1966). Sexuality was found predominantly in intermediate sized, low food level, brown animals. The green hydra were in general smaller than the brown.

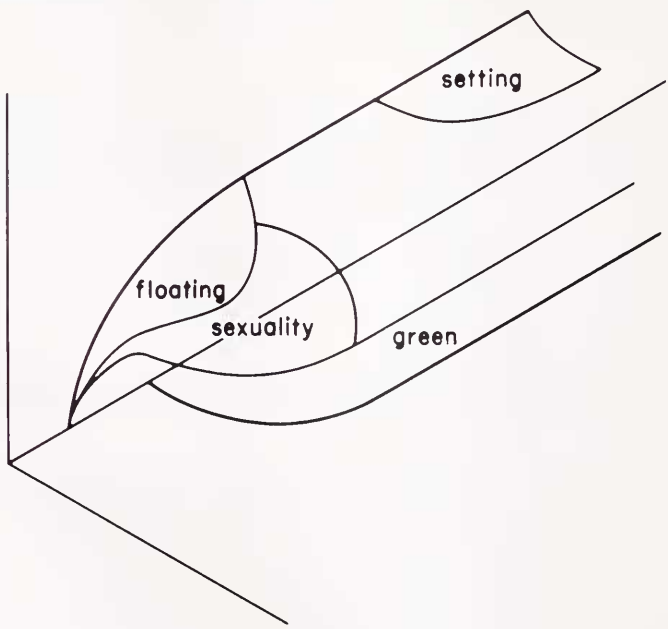

FIGURE 4. Localizations of physiological and behavioral properties on the surface of Figure 1 as hypothesized by Slobodkin (1979).

In short, position on the surface is related to physiological state, as predicted by Slobodkin (1979). Obviously, the ecological relationships of a floating animal are different than those of a settled animal in many ways. We have thus demonstrated an affirmative answer to the question of whether position on the surface matters both physiologically and ecologically.

Discussion

The third question stated in the introduction, (*i.e.*, the possible significance of these results), will now be addressed. The results will be discussed in four contexts—the idea of constraints in evolution; the relation between constraint systems and resource budgets; the search for other, similar, constraint systems; and finally the implications of our findings for the natural history of hydra.

Evolutionary constraint systems

Clutton-Brock and Harvey (1979), in their review of constraint systems, distinguish between "generic constraints" and "evolutionary constraints". Generic constraints are those sets of properties which are found to be correlated with physiological or ecological categorizations of organisms, without being, necessarily, confined to single taxonomic categories. For example, herbivory may imply the co-occurrence of one set of properties, while carnivory implies another. All homeotherms may share certain characteristics, all poikilotherms another. Evolutionary constraints, in contrast, are inferred from comparisons between members of different subcategories within a larger taxonomic category. We consider that we have demonstrated an evolutionary constraint system in hydra. Note, however, that both Clutton-Brock and Harvey (1979) and Gatto, Mattessi and Slobodkin (in prep.) discuss the fact that an apparent surface may actually consist of a series of separate surfaces, each perhaps representing a genotype or species, that resemble a single surface on the generic level in much the same way that the individual slats of a "Venetian blind" are seen as one surface from across the room. Our data are indeterminate on this issue.

Individual hydra can equilibrate at various locations on the surface as a consequence of environmental factors. The fact that, at least within the statistical limits of our data, different species share the same surface, leads us to believe that microevolutionary changes in hydra would tend to move them about on the surface rather than orthogonal to it.

Gould (1980) has presented the metaphor of objects resting on a surface to help explain what is meant by an evolutionary constraint. In this metaphoric context, denial of the existence of constraints on evolutionary direction is taken as imagining a ball rolling on a flat plane. This is taken by Gould and Lewontin (1979) as the image underlying what they refer to as the "Adaptationist Programme." How far the ball rolls depends only on the force with which it is pushed, not on the direction. Gould goes on to suggest that evolutionary changes for any particular kind of organism may be more restricted in their direction, resembling a polygonal solid, whose motion will depend on both force and direction of the propulsive forces, as well as on which of its faces it is resting. An actual polygonal solid cannot roll, but can be more readily tipped over in certain directions. In a sense we have explored this metaphor. We believe that on experimental and theoretical grounds we have demonstrated explicitly a set of ecological and physiological constraints on the genus *Hydra*. On the basis of this demonstration we suggest adding to Gould's metaphor

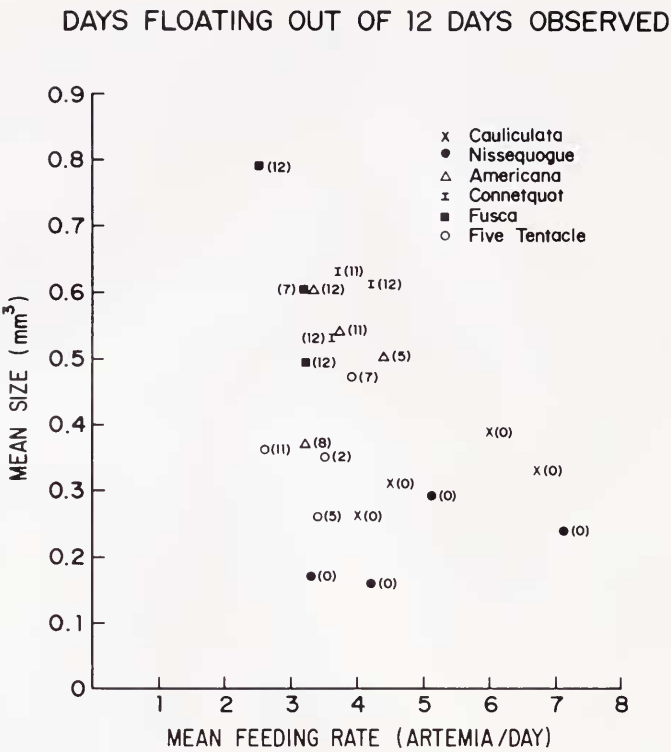

FIGURE 5a. The relation between fraction of days during which animals were floating, body size estimated photographically, and mean number of *Artemia* nauplii consumed. The *P* value associated with this distribution arising at random was determined by the Spearman Rank Correlation Coefficient of the order of the points when projected onto a line with a negative forty five degree slope and their order in floating rate. *P* was less than .001.

the image of a non-spherical solid with rounded edges, or perhaps no clear edges at all, which is capable of rolling easily in only certain directions, and must be toppled over if it is to roll in other ways. The mental image is that of the conical egg of the murre, which rolls in tight curves, thereby avoiding falling off ledges (Heinroth and Heinroth, 1958).

Constraint systems as consequences of resource budgets

There is an obvious connection between analyses of budgets and constraints and discussions of ecological and evolutionary "strategies." Various theories of evolutionary strategy build on the assumption that organisms are constrained so that their capacity to do a particular thing or have a particular property carries a "cost" which interferes to some degree with their capacity to do another thing or have another property. This approach is recently summarized by Townsend and Calow (1981) and McCleery (1978).

The analyses of energy, material, and time budgets for individuals and for populations demonstrate that there are restrictions on the present activities of organisms. Energy used for running can not be used for growth. Material used for seeds can

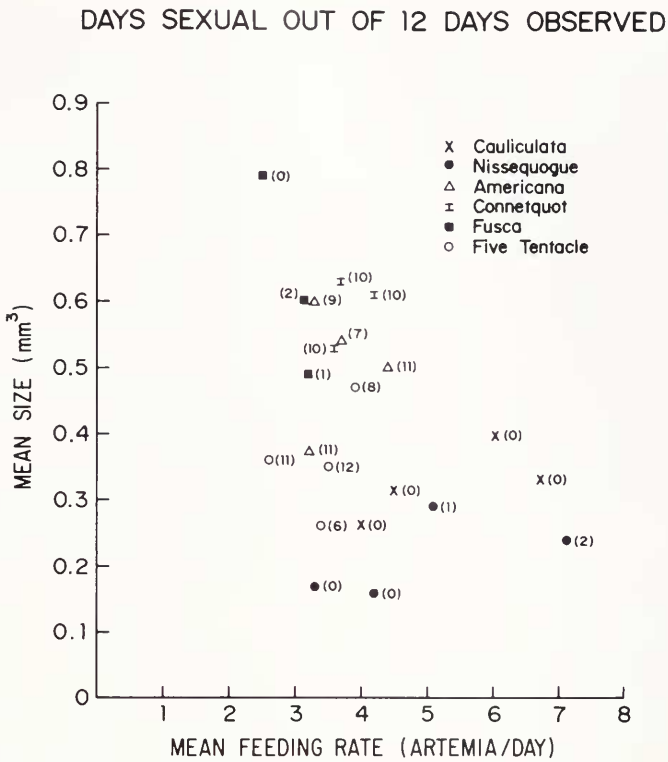

FIGURE 5b. The relation between the occurrence of gonads, body size and food consumption. The values are not randomly distributed ($.05 > P > .01$) nor are they monotonically distributed along the axes of food consumption and body size. Sexuality occurs most often at intermediate levels of food and body size.

not make leaves. Time spent preening can not be used for feeding, etc. A sufficient number of inverse correlations have been demonstrated between properties of organisms that excellent summaries now appear in elementary texts [for example, Begon and Mortimer's chapter on "Life history strategies" (1981)].

The observed constraint surface in hydra, which would be included in the category of "evolutionary constraints" of Clutton-Brock and Harvey (1979), may be considered an elementary consequence of energy budget considerations.

If any two activities or properties of a single organism require sufficiently large allotments or utilization rates of energy or some other resource, development of one of these properties will tend to inhibit or reduce the development of the other. If we consider several organisms, all similar in developmental and physiological potentialities, but differing somewhat as a result of environmental differences, then those individuals that have enhanced one of our hypothetical properties will to some degree have reduced the other. It is possible for organisms to have the same, or very similar anatomy and developmental properties, but to differ genetically in how they partition available resources between the two properties. In particular, this applies to organisms which are of different, but closely related species. In fact, the term "closely" in the previous sentence may be defined by the existence of such simi-

larities. Such pairs of properties meet Clutton-Brock and Harvey's criterion for being under evolutionary constraint. Only if the development of the pair of properties use different resources, or use resources very sparingly, can both properties be increased in the same organisms and under the same circumstances.

We are not confined to considering only pairs of properties. As larger sets of properties are taken into consideration the development of all the properties of the set is more and more likely to constitute a significant fraction of the organisms' resources, and constraints are more likely to become apparent over the set as a whole, whether they are in evidence for any pair of properties. Notice that any property that is found to always be enhanced as some other property is increased is likely to be artifactual, in the sense of Gould and Lewontin's (1979) discussion of the primate chin.

Assume that the degree of development of the properties in question can be measured in the same units as the resource income. If the income of energy, or any other resource, to an individual organism or population of organisms is known, then for any set of properties which are under physiological constraint, it is possible to construct a budget by assuming that the total supply of the resource in question allotted to the set of behaviors is equal to the measured income of that resource. The usual technique would be by multi-dimensional regression analysis. Examples and discussions of this procedure in this context may be found in Slobodkin (1980) and McFarland (1976).

The two properties, body size and budding rate in hydra both require the production and maintenance of tissue. The tissues of a bud are not noticeably different from those of its mother, and our data indicate that evolutionary constraint exists on this pair of properties. No hydra can simultaneously increase both its body size and budding rate above the constraint surface unless it can make a fundamental improvement in the efficiency of its biochemical processes. This apparently has not been possible. In this sense, the area above the constraint surface is free of hydra due to thermodynamic limitations.

Notice that green hydra have energy resources that are unavailable to brown ones. We estimated the amount of energy supplied by the algae, and this permitted us to consider green and brown hydra to be on the same surface. If we think in terms of a constraint set by animal food income, then the green hydra must be thought of as being above the constraint surface. We expect that there exists a constraint surface for all species of green hydra. In this sense, evolutionary loss or gain of the capacity to maintain symbiosis with algae would constitute a macro-evolutionary step for hydra.

The area beneath the surface is kept free of hydra by evolutionary considerations. Conceivably some hydra with a low capacity to maintain tissue and at the same time a low budding capacity could perhaps have some kind of selective edge. For example, hydra are unable to eat certain kinds of cladocera. One of these, *Anchistropus,* actually feeds on hydra (Hyman, 1926; Borg, 1935; Griffing, 1965; Personal Observation, L.S.). If *Anchistropus* were to become extremely common, we might expect that a strain of hydra that was immune to its attack, or even capable of feeding on it, might have a selective advantage. Under these circumstances we might expect that efficiency of growth and reproduction would be evolutionarily unimportant.

We have some evidence that aposymbiotic *Hydra viridis* might fall below the observed surface (Stiven, 1965; Pardy and Dieckmann, 1975; but see Cantor and Rahat, 1982). There is no evidence that aposymbiotic *Hydra viridis* occur in nature.

The search for other constraint systems

Raup and Stanley (1971) studying snail shell evolution, Hutchinson (1968) for Bdelloid rotifers, and Porter (1976) for some of the Scleractinian corals, among others, all have evidence for restrictions on evolutionary possibilities. Raup and Stanley present their data in the space defined by the mathematical representation for a coiling shell, which contains three parameters. Both Hutchinson and Porter present their data as clouds in two dimensions. On purely formal grounds it is understood that often data which appear as points on a surface of a given dimensionality will, when projected onto a space of lower dimension, appear as a cloud. Conversely, we believe that many of the taxonomically restricted scatter diagrams published in ecological literature will appear as surfaces if third or higher dimensions are added, and that some of these surfaces will permit mapping of particular physiological or behavioral properties. We expect that, while which, and how many, measurement axes will define a surface for a particular group of organisms is not obvious, all such sets of axes will share certain properties. We believe that they all will be related to resource budgets. One axis will consist of some resource and the others will be different ways in which that resource is expended. This will guarantee suitable concavity and monotonicity of the surfaces.

Principal components analyses test dimensionality. Our hypothesis, presented in Figure 1, assumes monotonic curves. Fortunately the rankit transformation maps monotonic curves onto flat planes, permitting our use of the Bartlett's test for sphericity. For reasons presented above, we expect that most evolutionary constraint surfaces will also project as monotonic curves in a space of sufficient dimensionality. In general, sufficient dimensionality will have been achieved in a constraint surface when rankit transformed data can be significantly explained by a number of components one less than the total number of measured variables. Principle components analysis, combined with either special tests, of the sort we used, or Monte Carlo simulations, may provide probability estimates for measuring the quality of the surfaces.

The natural history of hydra

Note that Figure 1 is drawn as if the entire surface were available for hydra. We believe that the edges will tend not to be occupied by actual organisms. This is due to the fact that the particular environmental problems which arise for hydra at various points on the surface are likely to differ.

Excessively large hydra have very high maintenance costs, so that budding can only occur if the food supply is very abundant. The capacity to float may permit these larger hydra to survive in an unpredictable environment. They are capable of surviving for an extended period without food. During this period floating animals may encounter richer concentrations of prey. Being excessively small probably narrows the range of possible food items and also narrows the time available for a hydra to starve between meals and still be large enough to capture prey. Floating until new feeding grounds are encountered does not seem as useful for small hydra, since not only is their ability to survive starvation while floating limited, but their range of acceptable animal foods is restricted. Symbiotic algae may serve small hydra in essentially the same way that floating serves large ones, since the symbionts extend the period that these animals can survive between feedings. Bossert and Slobodkin (1983), Thorington and Margulis (1980), and others (cf. Hyman, 1940; Kaenev,

1969) have shown that at least the largest of the green hydra may, under some circumstances, suffer damage from their algal symbionts. That is, at particular regions on this surface of constraints special ecological problems arise. Particular mechanisms for solving these problems have evolved. These include symbiotic algae supplementing the food supply and the capacity to float to richer food areas.

We believe that environmental changes may distort or rotate the constraint surface. We know that those species of hydra so far examined have a lower budding rate and larger body size at lower temperatures (Hecker, 1976) and that floating rate is sensitive to temperature (Slobodkin, 1979).

In hydra the empirical evidence suggests that a reasonably complete and explicit description of the constraints of both physiological and evolutionary responses consists of a surface embedded in a three dimensional space, on which physiological and behavioral properties may be mapped. We suggest the possibility that similar descriptions, consisting of a mapped surface in a minimum of three dimensions may exist in other groups of closely related species. It seems likely that physiological, developmental, or evolutionary alterations which result in movement on such a surface occur more frequently than alterations which successfully permit changes which are orthogonal to the surface. This may relate to the problems of the contrast between micro- and macro-evolution.

Constraint surfaces of this type may be viewed as consequences of resource budget considerations in groups of organisms that share most of their developmental and anatomical properties, but differ in their "Policy" (in the sense of Gatto, *et al.*, in prep) of apportioning resources to different uses. There is an intimate connection between evolutionary constraint surfaces, optimality theory, and resource budgets.

Acknowledgments

These studies were supported by grants from the Biological Sciences Division of the U. S. National Aeronautics and Space Agency, the Mobil Oil Foundation, and the Italian National Research Council. Profs. R. Armstrong, L. Ginzberg, J. Rohlf, and H. Lyman of Stony Brook provided criticism, encouragement, and advice. Scott Ferson, Dan Wartenburg, and Patricia Bossert, graduate students in the Ecology and Evolution Department each provided their own kind of help. Several undergraduate students were invaluable. These include Jay Fader, who did most of the photography, John Le Guyader and Heidi Chapnick who participated in the experimental work and who, along with Louise Holbrook helped in the tedious work of maintaining stocks. The animals from Central Park were provided by Mike Lewandowsky. R. De Bernardi of Pallanza, Italy, facilitated the collection of *Hydra fusca*. The 1st. di Genetica, Biochemica, ed Evolutionistica, C.N.R. at Pavia provided hospitality and an opportunity for discussion. This is contribution number 452 from the Ecology and Evolution Program, SUNY, Stony Brook.

LITERATURE CITED

Bartlett, M. S. 1950. Tests of significance of factor analysis. *Brit. J. Psychol.* (Statistical Section) **3**: 77–85.

Bateson, G. 1963. The role of somatic change in evolution. *Evolution* **7**: 529–539.

Begon, M., and M. Mortimer. 1981. *Population Ecology; A Unified Study of Plants and Animals.* Sinauer Associates. Sunderland, MA. 200 pp.

Borg, F. 1935. Zur kentniss der Cladoceran-gattung *Anchistropus. Zool. Bidr. Upps.* **15**: 289–330.

BOSSERT, P., AND L. B. SLOBODKIN. 1983. Thee effect of fast and regeneration in light vs. dark on regulation in hydra-algal symbiosis. *Biol. Bull.* **164**: 396–405.

CANTOR, M. H., AND M. RAHAT. 1982. Regulation of respiration and photosynthesis in *Hydra viridis* and in its separate cosymbionts: Effect of nutrients. *Physiol. Zool.* **55**: 281–288.

CLUTTON-BROCK, T. H., and P. H. HARVEY. 1979. Comparison and adaptation. *Proc. R. Soc. Lond. Ser. B* **205**: 547–565.

GATTO, M., C. MATESSI, AND L. B. SLOBODKIN. (In prep.) Evolution within ecological and physiological constraints: Explicit predictions for hydra.

GOULD, S. J. 1980. The evolutionary biology of constraint. Daedalus, *Proc. Am. Acad. Arts Sci.* **109**: 39–52.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc. Roy. Soc., London, Ser. B* **205**: 581–598.

GREEN, P. E., AND J. DOUGLAS CARROL. 1978. Pp. 361–364 in *Analyzing Multivariate Data.* Dryden Press. Hinsdale, IL.

GRIFFING, T. 1965. *Dynamics and Energetics of Brown Hydra.* Ph.D. Thesis in the Department of Zoology, University of Michigan, Ann Arbor.

GURKEWITZ, S., M. CHOW, AND R. D. CAMPBELL. 1980. Hydra size and budding rate: influence of feeding. *Int. J. Invert. Reprod.* **2**: 199–201.

HECKER, B. 1978. *Adaptive Responses in* Hydra oligactis. Ph.D. Thesis in the Department of Ecology and Evolution, S.U.N.Y., Stony Brook.

HECKER, B., AND L. B. SLOBODKIN, 1976. Responses of *Hydra oligactis* to temperature and feeding rate. Pp. 175–183 in *Coelenterate Ecology and Behaviour,* G. O. Mackie, ed. Plenum Press, New York.

HEINROTH, O., AND K. HEINROTH. 1958. *The Birds.* University of Michigan Press, Ann Arbor, MI.

HUTCHINSON, G. E. 1968. When are species necessary? Pp. 177–186 in *Population Biology and Evolution,* R. C. Lewontin, ed. Syracuse University Press.

HYMAN, L. 1926. Note on the destruction of hydra by a Chydorid Cladoceran, *Anchistropus minor* Birge. *Trans. Am. Microsc. Soc.* **45**: 298–301.

HYMAN, L. 1940. *The Invertebrates: Protozoa through Ctenophora.* McGraw-Hill Book Company, NY 726 pp.

KANAEV, I. I. 1969. *Hydra: Essays on the Biology of Freshwater Polyps.* Translated by E. T. Burrows and H. M. Lenhoff; H. M. Lenhoff, editor and publisher. Miami. 452 pp.

LENHOFF, H. M., AND R. D. BROWN. 1970. Mass culture of hydra: an improved method and its application to other aquatic invertebrates. *Lab. Anim.* **4**: 139–154.

LOMNICKI, A., AND L. B. SLOBODKIN. 1966. Floating in *Hydra littoralis. Ecology.* **47**: 881–889.

MCFARLAND, D. J. 1976. Form and function in the temporal organization of behaviour. Pp. 55–93 in *Growing Points in Ethology,* P. G. Bateson and R. A. Hinde, eds. Cambridge University Press.

MCCLEERY, R. H. 1978. Optimal behaviour sequences and decision making. Pp. 377–410 in *Behavioural Ecology, an Evolutionary Approach,* J. R. Krebs and N. B. Davis, eds. Sinauer Associates. Sunderland, MA.

MUSCATINE, L. 1961. Symbiosis in marine and freshwater coelenterates. Pp. 255–264 in *The Biology of Hydra and Some Other Coelenterates,* H. M. Lenhoff and W. F. Loomis, eds. University of Miami Press, Coral Gables.

OTTO, J. J., AND R. D. CAMPBELL. 1977. Tissue economics of hydra: regulation of cell cycle, animal size, and development by controlled feeding rates. *J. Cell Sci.* **28**: 117–132.

PARDY, R. L., AND C. DIECKMANN. 1975. Oxygen consumption in the symbiotic hydra *Hydra viridis. J. Exp. Zool.* **194**: 373–378.

PLOTKIN, H. C., AND F. J. ODLING-SMEE. 1981. A multiple level model of evolution and its implications for sociobiology. *The Behavioral and Brain Sciences* **4**: 225–268.

PORTER, J. W., 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *Am. Nat.* **110**: 731–742.

RAUP, D. M., AND S. M. STANLEY. 1971. *Principles of Paleontology* W. H. Freeman and Co., San Francisco. 388 pp.

ROHLF, F. J., AND R. R. SOKAL. 1969. *Statistical Tables.* W. H. Freeman and Co., San Francisco. 253 pp.

ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1982. NT-SYS, numerical taxonomy of multivariate statistical programs. *Technical Report,* State University of New York, Stony Brook.

SLOBODKIN, L. 1980. *Growth and Regulation of Animal Populations,* Second Enlarged Ed. Dover Publications Inc., New York. 234 pp.

SLOBODKIN, L. 1964. Experimental populations of Hydrida. In British Ecological Society Jubilee Symposium, A. Macfadyen and P. J. Newbould, eds. *J. Anim. Ecol.* **33**(Suppl.): 131–148.

SLOBODKIN, L. B. 1979. Problems of ecological description: The adaptive response surface of hydra. In *Proc. Symp. "Biological and Mathematical Aspects of Population Dynamics,"* R. de Bernardi, ed. Mem. Ist. Idrobiol. Suppl. **37**: 75–93.

SLOBODKIN, L. B., AND A. RAPOPORT. 1974. An optimal strategy of evolution. *Q. Rev. Biol.* **49**: 181–200.

STIVEN, A. E. 1965. The relationship between size, budding rate, and growth efficiency in three species of hydra. *Res. Popul. Ecol.* **7**: 1–15.

THORINGTON, G., AND L. MARGULIS. 1981. *Hydra viridis;* Transfer of metabolites between hydra and symbiotic algae. *Biol. Bull.* **160**: 175–188.

TOWNSEND, C. R., AND P. CALOW, eds. 1981. *Physiological Ecology: An Evolutionary Approach to Resource Use.* Sinauer Associates, 393 pp.

WRIGHT, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. Sixth Intern. Cong. Genetics.* **1**: 356–366.